

ON THE INTERPRETATION OF CERTAIN FEATURES OF AN EMBRYONIC SKULL OF PLATYPUS.

By H. LEIGHTON KESTEVEN, D.Sc., M.D.

(Nine Text-figures.)

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The present work was undertaken with the object of investigating further the development of the bone which de Beer and Fell (1936) identified as the alisphenoid. In collaboration with Furst, the author (1929) had described the basisphenoid as being developed from three centres of ossification, a central and two lateral. It appeared that it was these latter which de Beer and Fell had identified as the alisphenoid bones.

The study of the sections revealed several features of such interest that it was decided to model portion of the platypus head with a view to investigating these.

Material.—Besides the specimens which were used by the author and Furst in a previous study of the late embryonic skull (Kesteven and Furst, 1929), the head of an embryo measuring 140 mm. from tip of snout to end of tail along the dorsal surface was studied in sagittal and transverse sections. I have to thank Professor C. W. Stump for the opportunity to study this specimen and for its preparation. The head was cut off and then divided along the mid-sagittal plane into two halves. One half was cut in the sagittal plane, the other in the transverse vertical. A model was reconstructed from trans-sections numbers 227 to 327 inclusive. This model included, as well as the chondrocranium, portions of the parasphenoid (the mammalian pterygoid) and dentary bones, the second, fourth, fifth and seventh nerves, the internal cerebral and orbital branches of the carotid artery, portion of the large anterior ventral venous sinus with the commencement of its main efferent vein, and portion of the pituitary gland.

The model was made with a slight modification of the blotting paper wax method. Outlines were obtained by using a vertically arranged projecting lantern made for the purpose; they were coloured differentially for the various structures and cemented together with rubber solution. The adherence of the sections was all that could be required, but only after the surfaces had been coated with the solution twice, allowing the first coat to dry before applying the second.

The magnification of the model is twenty diameters. The portion included in the model measures 5 mm., one hundred sections, each 50μ thick. The model is 10.5 cm. long, that is to say, it is 0.5% over-long, a distortion so slight as to be negligible.

The sections will be returned to the Launzelot Harrison collection in the Anatomy Department at Sydney University, and the model will be lodged with them.

The embryo is No. T.O.4 in that collection, and the head has been catalogued as "Head of *Platypus* MM". The crown-rump measurement is approximately 56 mm., the snout-tail measurement approximately 140 mm.

I should like to thank Dr. A. A. Abbie for his assistance in the identification of the cranial nerves. My thanks are also offered Professor Burkitt as well as Professor Stump for the opportunity to use material from their departments at Sydney University. I have also to thank the Executive of the Directorate of The Goodyear Tyre & Rubber Co. (Australia) Ltd. for the equipment of my laboratory, wherein most of the work was done.

The Alisphenoid Problem.

In 1918 the author pointed out that there was strong evidence in favour of recognizing the "echidna-ptyergoid" as the homologue of the tympanic wing of the mammalian alisphenoid. This was to a certain extent in agreement with a conclusion previously arrived at by Watson (1916), differing therefrom in that I was unable to agree that the mammalian alisphenoid was derived from the processus ascendens quadrati; de Beer and Fell were, therefore, in error in stating (1936, p. 21) that I had equated the echidna pterygoid with the processus ascendens.



Figs. 1, 2 and 3.—Transverse sections Nos. 261, 259 and 257 through the right half of the head of a *Platypus* embryo measuring 25 mm. from tip of snout to occiput.

De Beer and Fell (1936, p. 21) state that "a perichondral ossification is present in the ala temporalis, distinct from the alisphenoid. And since this alisphenoid is present in addition to and distinct from the 'Echidna-ptyergoid', the *Echidna-ptyergoid* cannot be the alisphenoid."

I find that there is a definitely endochondral ossification of the processus alaris medially to the canal for the stapedial artery. This ossification takes the form of an almost continuous subchondral lamina, as indicated in Figures 1, 2 and 3, and spicular bone formation extending deeply into the cartilage. Posteriorly, medial to the exit of the artery (Fig. 1), the ossification does not reach the medial wall of the groove in which the artery lies, nor does it reach deeply to the medial wall of the canal itself (Fig. 2), but just in front of the canal it forms the medial wall of the groove (Fig. 3).

The relation to the vidian nerve is of particular interest. In this 140 mm. embryo the ossification lies lateral to and just clear of the nerve, but the vidian

canal is formed below the nerve by this ossification laterally and the pterygoid bone medially.

In this embryo there is no sign as yet of the medial area of ossification of the basisphenoid.

The next older embryo available for study is the 175 mm. specimen which was studied in 1929.

This is the specimen on which was based the statement that the basisphenoid ossifies from three centres; unfortunately the bald statement alone was made at that time. The lateral ossification in this skull has extended to enclose, almost completely, the arterial canal, and medially just on to the inferior surface of the horizontal portion of the basisphenoid cartilage. It will be noted that this extension is such that the whole of the vidian canal is now enclosed laterally by this ossification.

The prepared skull of this last specimen measures 25 mm. from the tip of snout to the occipital condyles. The next larger head measures 48 mm. In this the whole basisphenoid is completely ossified and there is no trace of any suture; on the contrary, there is complete fusion of the three centres of ossification. This last specimen was probably older than the 250 mm. embryo studied by Watson, in which also the three areas were completely fused, so much so, in fact, that there was no evidence of other than one continuous ossification.

When it is remembered that throughout the whole of the lower vertebrata the basisphenoid is ossified from two lateral centres of ossification, situated on either side of and, commonly, behind the pituitary fossa, the lateral areas in the basis cranii of the present embryos are at once recognizable as the two familiar areas of the saurians.

Almost without exception, in the mammalian skulls, one will observe that there remains a meniscus of cartilage between the developing alisphenoid and the lateral edge of the basisphenoid ossification. This meniscus is completely wanting; not only is this so, but those sharply-defined contiguous edges of ossification of the two bones in early stages of development are also completely missing in these embryos.

There is a still further difference observable. In most, if not all, mammals and marsupials the ala temporalis is rapidly ossified throughout its thickness, so that once ossification is fully under way one observes the basisphenoid and alisphenoid separated by the meniscus of cartilage at their contiguous edges. In the *Ornithorhynchus* embryos the median area of ossification develops on both surfaces of the cartilage, whilst the lateral areas extend on the ventral surface so as almost to meet the median area before the dorsal surface of the cartilage is ossified. From the appearances of the two younger embryos studied it would appear that fusion of the lateral and central areas takes place before the dorsal surface of the cartilage is ossified laterally.

From the foregoing evidence it is concluded that the basisphenoid bone in *Ornithorhynchus* is ossified from three centres, as previously stated, and that de Beer and Fell were in error when they thought to recognize the alisphenoid in the lateral area of ossification.

Before leaving this question it should be noted that the identification of the lateral area of the ossification as the alisphenoid, introduces the utmost confusion into the arguments relative to the homology of the mammalian pterygoid in the Monotremes.

This bone was identified as the lateral wing of the parasphenoid by Gaupp, and his conclusion has been accepted by most workers since his statement of the case appeared. It must, however, be remembered that the most weighty evidence on which the identification rested was that the bone closed the vidian canal ventrally. Now it has been very generally recognized that the vidian canal is that part of the parabasal canal which lies between the parasphenoid and the basisphenoid.

There is no doubt whatever that in *Ornithorhynchus* the vidian canal lies between the lateral ossification and the mammalian pterygoid; therefore, if this lateral ossification be the alisphenoid bone, then the vidian canal lies between the processus ascendens quadrati and the parasphenoid, that is, for all those who believe that the alisphenoid is derived from the ascending process.

This amounts to a *reductio ad absurdum*, for such a situation for a vidian canal is clearly an impossibility, if only because the parasphenoid could not come to underlie the processus ascendens.

This has not been cited as evidence against the identification of de Beer and Fell because the author (1) is unable to regard the alisphenoid as having been derived from the ascending process, and (2) has pointed out that in most primitive reptiles the vidian canal lies between the pterygoid bone and the parasphenoid; he therefore (3) concludes that the reptilian pterygoid and mammalian pterygoid are homologous, and (4) has also advanced reasons for believing that both these are derived from the parasphenoid bone.

*The Relation of the Cranial Nerves and the Stapedial Artery
to Certain Cranial Structures. Figs. 4, 5, 6.*

The second nerve was traced from the chiasma forward through the peripituitary venous sinus and out of the cranial cavity through the pseudoptic foramen close to the floor. It then passes rostrad and laterad below the ophthalmic division of the fifth, and continuing in the same general direction, but with an inclination dorsad, reaches the eyeball.

The third nerve was exceedingly difficult to find and was not traced very far. It arises from the medial edge of the peduncle above, that is to say, anterior to, the interpeduncular ganglion and passes ventrad, laterad and rostrad in a fold of pia mater to reach the dorsal surface of the fifth nerve roots close to their junction with the ganglion. From here it was traced only a very short distance. It is confidently believed that it passes out of the cranial cavity in company with the first and second divisions of the fifth nerve behind and lateral to the processus clino-orbitalis. There is no doubt whatever that it does not emerge in front of the process through the pseudoptic foramen as stated heretofore.

The fourth nerve was traced from the lateral portion of the anterior medullary velum. It passes down close to the median surface of the backwardly-projecting posterior pole of the cerebral hemisphere and comes to lie upon the dorso-medial surface of the processus clino-orbitalis. The nerve continues forward and laterally, almost maintaining a constant level, so that, as the process inclines dorsad, the nerve passes below it and passes out between the process and the dorsal surface of the ophthalmic nerve. It crosses the nerve and then inclines ventrad so as to lie lateral to, and almost at the same level as, the optic nerve.

The very large roots of the fifth nerve are striking objects. It may be of interest to record that the motor division emerges at an appreciable distance from the sensory as a single root. The point of emergence is slightly anterior

to the motor root, and medially and dorsally thereto. This division of the nerve maintains its anatomical independence throughout its course; its branches do not commingle with those of the sensory division. The nerve may be very easily traced passing out laterally between the sensory roots and the floor of the cranium, then between the Gasserian ganglion and the roof of the cavum cochleare. Beneath the point of division of the mandibular ramus from the other two, the motor division turns sharply dorsad and rostrad and shortly thereafter it breaks up into its component nerves.

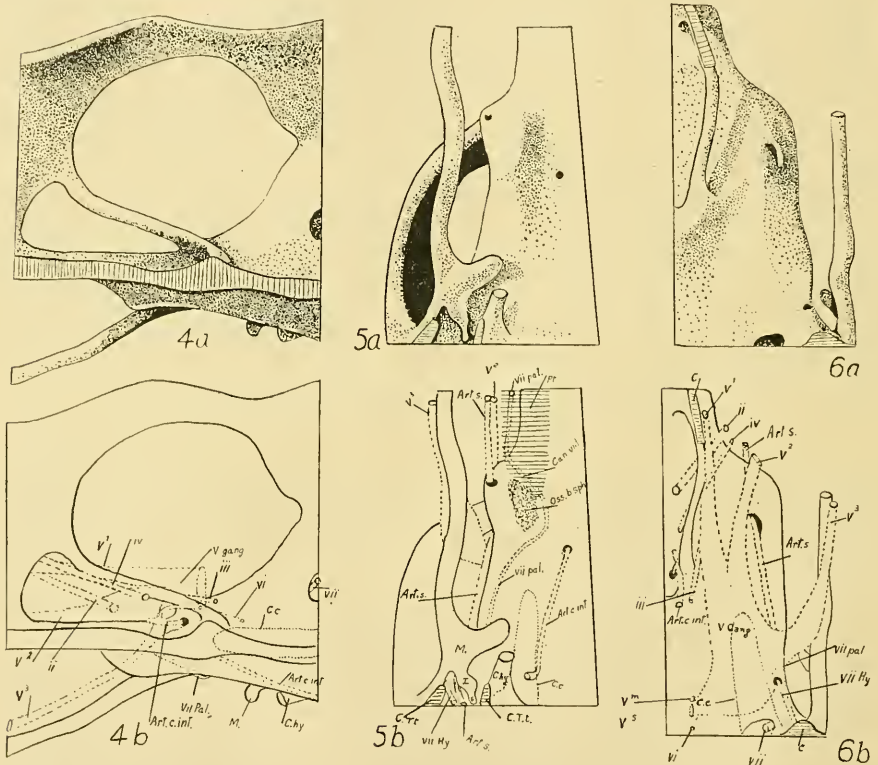


Fig. 4.—4a, Medial aspect of the model reconstructed from sections Nos. 227 to 327. 4b, Outline of same with the position of nerves and vessels indicated in dotted lines. (All the structures indicated, except nerves 3 and 6, are included in the model.)

Fig. 5.—5a and 5b, Ventral view and outline with nerves and vessels.

Fig. 6.—6a and 6b, Dorsal view of the cranial floor, with the roof removed, and outline showing the situation of the nerves and vessels.

The sixth nerve emerges from the ventral surface of the medulla medial to and in front of the roots of the seventh. The nerve passes ventrad and rostrad and then rostrad and laterad along the floor of the cranium. It is believed that it emerges from the cranium beneath the fifth nerve and courses forward ventral to the first branch, but it was lost almost as soon as it penetrated the membranous lining of the cranial cavity.

The seventh nerve passes almost directly into the anterior notch of the widely open internal auditory meatus, and then traverses the roof of the cavum

cochleare in a direction forward, laterally and slightly ventrally. The geniculate ganglion lies against the lateral wall of the cavum cochleare close to the exit of the nerve from the facial canal. From this point the palatine, vidian, nerve runs forward around the lateral edge and on to the ventral surface of the basis cranii. Below the basisphenoid region the nerve lies close to the medial edge of the lateral ossific centre of the basisphenoid bone, covered ventrally by the pterygoid. In my model the lateral portion of the pterygoid has been omitted in order to expose the nerve.

The ramus hyomandibularis runs caudad and very slightly laterad and passes below the malleo-otic commissure and above the incus and stapes, and then turns sharply ventrad behind the last two structures.

The stapedia artery lies below the hyomandibular nerve as they pass together medially to the tegmen tympani and between the incus and malleo-otic commissure.

The Processus Clino-orbitalis.

This has recently been identified by de Beer and Fell (1936) as the pila antotica. They remark: "It may be noted that the Monotremes are the only mammals in which the pila antotica is preserved, and it is therefore of additional interest to find that its morphological relations are similar to those found in the Reptiles. It is situated behind the oculomotor and trochlea nerves and the pituitary vein and in front of the trigeminal and abducent nerves." They further state that, in the Platypus, "the dorsum sellae" . . . "is directly continuous with the pila antotica on each side, just as it (or its homologue the crista sellaris) is in *Lacerta*".

The statement is inaccurate in more respects than one. Firstly, this pila is situated in front of the oculomotor nerve. Secondly, the suggestion that the abducent nerve lies behind the pila antotica is quite wrong, if it is intended to convey the idea that the nerve emerges from the cranium behind the pila. Thirdly, the pila antotica is not nearly so directly continuous with the crista sellaris as is the clino-orbital process with dorsum sellae.

Actually the relations of the structures to the process are, in the main, such as to contra-indicate the equation of de Beer and Fell.

In the saurians the pila metoptica lies between the optic and the oculomotor and trochlear nerves. It arises from the basis cranii just forward of and laterally to the hypophysis and passes dorsally and *forward* with little lateral inclination to become attached to the orbital cartilage.

In the saurians the pila antotica lies between the oculomotor and trochlear nerves in front and the trigeminal nerve behind. It arises from the extreme edge of the basis cranii a little distance lateral to and, commonly, a little in front of or a little behind the crista sellaris at the posterior boundary of the pituitary fossa. From this point the process extends dorsally and laterally with an inclination *caudad* either to join the taenia marginalis close to the antero-dorsal corner of the otocrane or that corner of the otocrane itself, or ends freely above.

If the processus be any of the saurian pilae retained in a modified form, then it appears more correct to equate it with the pila metoptica than with the antotic pila.

Actually it differs from the former far less than from the latter. It has in front of it one single nerve which lies behind it in saurians, otherwise its relation to the nerves is identical. Its direction is very emphatically that of the metoptic pila rather than that of the antotic and so also is its dorsal connection.

The relation to the pituitary vein is certainly against such an interpretation, but, even so, it is still possible to regard the process as a not very markedly modified metoptic pila.

When compared with the antotic pila, we find that this is in front of two nerves which should pass in front of the antotic pila at their point of emergence from the cranium; it arises from the lateral end of the dorsum sellae, that is, from the dorsal surface of the trabecular plate instead of from the edge of the trabecula or from the trabecular crest; and, finally, its direction is quite different and its dorsal attachment without parallel amongst the saurians. Briefly, at best it can only be regarded as a very profoundly modified pila antotica.

The Ossicula Auditus.

Lightoller (1939) has just advanced reasons for the belief that the malleus is the homologue of the quadrate and not of the articular. The conditions in the present embryo may be interpreted as giving strong support to that contention. They do not, however, appear to throw any further light on his suggestions as to the derivation of the incus, but rather raise an altogether new concept on the question.

When the model of the chondrocranium was made it became apparent that Meckel's cartilage was continuous with the chain of auditory ossicles and also with the otocrane. Further than this, it was at once apparent that the connection with the otocrane was by way of the malleus.

Now, here was a peculiarity. Reichert's theory recognized the malleus as the articular. If, then, this be the articular, how came it to be directly continuous with the cartilaginous skull. The articular is an ossification of the proximal end of Meckel's cartilage, and the quadrate stands between it and the skull.

If, as Lightoller suggests, the malleus be the quadrate, this connection becomes at once understandable, for throughout the whole of the amphibians the quadrate is in direct cartilaginous continuity with the skull.

With a view to investigating the question as thoroughly as a single specimen permitted, a larger model of the auditory ossicles was built. This is thirty times as large as the structures modelled. The structures were found in sections Nos. 298 to 326. The model should, therefore, have measured 4.35 cm. from front to back; actually it measures 4.5 cm.—a negligible distortion (Fig. 7).

Since it was unlikely that the articular had acquired a cartilaginous connection with the skull, this connection was deemed to be one of the quadrate attachments, and with this in mind the model was compared with the saurian quadrate. This comparison failed to yield any explanation of the attachment because the quadrate is not so attached to the cartilaginous cranium in any of the saurians.

Comparison with the amphibian quadrate, however, seemed to provide an explanation.

The model exhibits the following features: Without being appreciably thickened from side to side, the proximal end of Meckel's cartilage is quite suddenly widened in the dorso-ventral plane. The upper level of the cartilage is maintained nearly constant, but there is a slight inclination dorsad, and after a short interval the cartilage is continued backwards at what appears to be a resumption of the original shape. This, which has been designated the malleo-otic commissure, joins the otic capsule. The point of junction is opposite the internal auditory meatus; it is, therefore, situated close to the posterior end of the cavum cochleare and the anterior end of the cavum vestibulare where these lie one above

the other. The tegmen tympani springs from the outer wall of the otocrane immediately behind and below the point of attachment. The expanded portion of the cartilage is without doubt the malleus, and the manubrium stands down and inward, medially, from the body of the future bone. Immediately below the malleolar end of the commissure a stout process projects directly backwards from the body of the malleus. This, which is identified as the incus, maintains its thickness for only a short distance, then commences to taper and at the same point inclines mediad and terminates at the fenestra ovalis.

On the median surface of the body of the malleus just behind the point of junction with the commissure a thick boss projects medially. Seen from above, this appears as an abrupt thickening of the upper edge of the cartilage. From

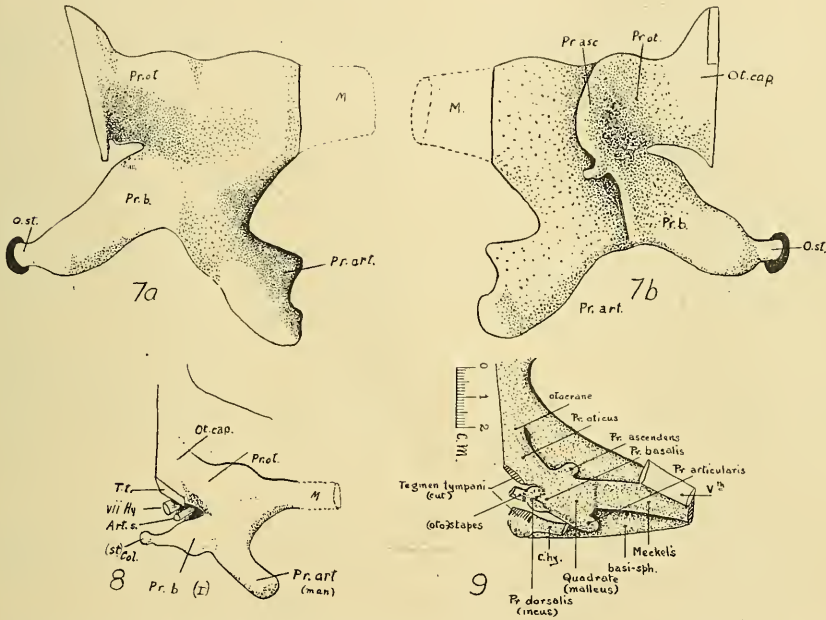


Fig. 7.—7a, Lateral, and 7b, medial view of the model of the auditory cartilages reconstructed from sections Nos. 298 to 326.

Fig. 8.—The auditory cartilages attached to the otocrane, showing the situation of the hyomandibular nerve and the stapedia artery, between the processus oticus and the processus basalis.

Fig. 9.—Oblique view of model, showing the cartilages of the middle ear. The probable location of the future lines of division and the joints are schematically indicated. This drawing is by Dr. Lightoller.

below or in front, this boss is seen to be excavated anteriorly, and from the medial aspect it is found to lose in antero-posterior thickness, and in height from the body of the cartilage, from above downwards. In the middle of its dorso-ventral length there is a small, backwardly projecting spicule of cartilage on its free edge (Fig. 7b).

Before proceeding to the comparison with the amphibian condition it may be remarked that none of the recent saurians can be regarded as ancestral to the mammals, the Chelonians alone being sufficiently generalized to be regarded as

approaching the ancestral type. Therefore, if there be reason to believe that amphibian processes of the quadrate are recognizable in the malleus of the Platypus, their presence need not be regarded as a recurrence of the amphibian feature. On the contrary, they may be regarded as persistent features, carried down through the ancestral type, in which (e.g. the Cynodonts) the quadrate was even more amphibian in character than is that of the chelonians.

In the Amphibia the quadrate is attached to the skull by three processes, ascending, otic and basal.

The otic is attached to the otocrane well above the level of the basis cranii and in front of the basal process. The stapedial artery runs forward and the hyomandibular branch of the facial nerve backward between these two processes, close to the otocranial wall with the body of the quadrate lateral to them.

The resemblance of the malleo-otic commissure and the incudal process to these two processes of the amphibian quadrate is such as to suggest very strongly that they are homologous structures (Fig. 8).

The resemblance does not cease here. The amphibian quadrate carries, below the otic process, a larger or smaller remnant of the palatal process, and the ascending process is either attached to the quadrate directly just above the palatal process or rises from the palatal process close to the body of the cartilage.

The larger model shows that there is a short stout process on the antero-medial and superior edge of the malleus. This short process is certainly in just the position where the ascending process should be found if this be a quadrate, and moreover the spicule of cartilage attached to this vestigial "ascending process" may be interpreted as a more vestigial palatal process.

The resemblance goes even further than this. If one detach the stapedial component from the medial end of the incudal process and Meckel's cartilage from the distal end of the mass, there remains, attached to the skull by the otic process only, a quadrate, in which one may recognize not only all the three processes of attachment, but also the main articular ramus of the cartilage, this last being, of course, the manubrium.

It is, therefore, concluded that in *Ornithorhynchus* the malleus is derived from the quadrate, that the incus is derived from the processus basalis quadrati, and that the manubrium mallei is derived from the ramus articularis quadrati. It is believed that the stapes is the oto-stapes of lower vertebrata.

It is probable that the first reaction to this interpretation of the ossicula auditus will be that it is far too much to expect so simple an explanation, and modifications of the quadrate so slight as to permit of the recognition of all the features of the primitive amphibian bone. Actually, however, therein lies much of the strength of the suggestion.

Reichert's theory is faced with the same difficulties as the theory here advanced and with others as well. Under both assumptions it becomes necessary to explain the fusion of the whole chain of ossicles in this cartilaginous stage; for this fusion no explanation is apparent.

Reichert's theory is implicit with the belief that the articulo-quadrate joint was abruptly abandoned as the functional joint of the jaw, and was converted at once into the malleo-incudal joint. This appears to be a necessary assumption under this theory, for it is difficult to understand how otherwise the joint could have been preserved. Further, if the joint be the articulo-quadrate joint, then the body of the incus must be regarded as the ramus articularis quadrati, and it becomes necessary to postulate the addition of the manubrium mallei from

some other source. In the present instance there is added the difficulty of explaining the cartilaginous continuity of the malleus and the otocrane. It is difficult to understand how the portio articularis of Meckel's cartilage can have grown past the quadrate, which intervened, to reach the skull. Further, it becomes necessary to assume that the articulo-quadrate joint was obliterated by a cartilaginous continuum and was then re-established. A still further difficulty presents itself. The articular bone is altogether external and lateral to the membrana tympani, so that it becomes necessary to assume the destruction of the primitive membrane and its replacement by a newer one, or to assume that the articular has, in some way, come to penetrate the membrane without leaving any trace of the involution and closing of the perforation.

It is assumed here that the fusion of Meckel's cartilage and the quadrate took place between the body of the latter and the proximal end of the former, and that this took place after the temporo-dentary joint had commenced to function. It seems reasonable to believe that after the articulo-quadrate joint ceased to function, the portio articularis and its bone should become vestigial and disappear. The quadrate, however, was probably attached to the membrana tympani, as in most Chelonians. It is assumed that it retained this relation to the membrane as it became gradually reduced in size. The later development of a newer os tympani replacing the original functional attachment of the quadrate, the development of the joint between the root of the processus basalis and the newer relation to the oto-stapes are stages in the evolution which we have no information about. Since two of these three changes must be simply postulated under Reichert's theory, as under this, they are difficulties common to both.

Lightoller (1939) has suggested that the incus is derived from the dorsal process of the oto-stapes. He has kindly handed to me the accompanying drawing (Fig. 9), which schematically applies his suggestion to this stage of the platypus ear.

The suggestion is very tempting and offers a simple explanation of the joint between the future malleus and the incus. It is, however, not accepted unreservedly here because the model of the future ear ossicles suggests that the joint between the malleus and the incus will develop right across the cartilage in front of the boss which has been identified as the processus ascendens.

Even if that be so, it may still be the fact that the processus dorsalis of the oto-stapes has been incorporated, and that incorporation has conditioned the development of the joint at the point of fusion with the quadrate and its extension through the bases of the processes of the quadrate.*

I should like to thank Professor A. N. Burkitt and Dr. G. H. S. Lightoller for their advice and criticism of this work.

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* This interpretation of the origin of the ossicula auditus is not novel. Dr. Lightoller has drawn my attention to the fact that Huxley, in his *Manual of the Anatomy of Vertebrated Animals* (1871, pp. 66 and 67), derived the malleus from the quadrate and the incus from the dorsal process of the otostapes. This, Lightoller remarks, is surprising for these views were not expressed by Huxley in his paper on the subject which appeared in 1869.

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Abbreviations used on the drawings.

Ali., Alisphenoid bone (Echidna-pterygoid); *Art.C.int.*, Internal cerebral artery; *Art.s.*, Stapedial Artery; *B.sph.* and *Oss.b.sph.*, Lateral area of ossification of the basi-sphenoid bone; *Can.vid.*, Vidian canal; *C.c.*, Cavum cochleare; *C.hy.*, Cerato-hyoid cartilage; *C.T.t.*, Tegmen tympani (cut away); *Dent.*, Dentary bone; *M.*, Meckel's cartilage; *Ot.cap.*, Otic capsule; *O.St.*, Oto-Stapes; *Pal.*, Palatine bone; *P.cl-o.*, Processus clino-orbitalis; *Pr.art.(Man.)*, Processus articularis quadrati (Manubrium); *Pr.asc.*, Processus palatinus, or perhaps processus ascendens quadrati; *Pr.b.(I.)*, Processus basalis quadrati (Incus); *Pr.ot.*, Processus oticus quadrati; *P.sph.*, Parasphenoid bone; *Pt.*, Pterygoid bone; *T.t.*, Tegmen tympani (cut away); vii *Hy.*, Hyomandibular branch of the viith nerve; vii *Pal.*, Palatine branch of the viith nerve.